

The first description of dinosaurian eggshell from the Maastrichtian Lance Formation, Wyoming, North America

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Van der Linden, T.T.P., Wallaard, J.J.W., de Rijke, M., and Fraaije, R.H.B. 2025. The first description of dinosaurian eggshell from the Maastrichtian Lance Formation, Wyoming, North America. *Acta Palaeontologica Polonica* 70 (3): 573–579.

Although numerous fossils have been excavated and described from the Upper Cretaceous (Maastrichtian) Lance Formation, eggs and eggshell remains are rare and have yet to be described in detail. Here, we provide the first description of an eggshell found in the Lance Formation in eastern Wyoming. The eggshell can be attributed to the oofamily Ovaloolithidae, and is most comparable to the oogenus *Ovaloolithus* based on the smooth outer surface, the eggshell thickness, the closely packed shell units, and the presence of two layers. The eggshell can tentatively be ascribed to either ornithopod or non-avian theropod dinosaurs. This new eggshell expands our understanding of the geographical distribution of ovaloolithid ootaxa throughout the uppermost Cretaceous of North America, having been previously described from the Maastrichtian North Horn Formation of Utah.

Key words: Ovaloolithidae, Dinosauria, eggs, Maastrichtian, Lance Formation, Wyoming.

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Received 23 September 2024, accepted 9 July 2025, published online 18 September 2025.

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Introduction

Dinosaur eggs and eggshell remains are important body fossils (e.g., Bertling et al. 2006, 2022; Lawver and Jackson 2014), as they provide information on reproductive behavior (e.g., Sellés and Galobart 2016), nesting conditions (e.g., Tanaka et al. 2018), and nesting environments of dinosaurs (He et al. 2019, 2020). In addition, dinosaur eggs inform on the faunal biodiversity of past ecosystems, especially when skeletal remains are lacking (e.g., Tanaka et al. 2016; Uematsu et al. 2023). On the North American continent, fossiliferous Cretaceous deposits are common, including formations preserving egg and eggshell material (e.g., Carpenter 1982; Hirsch and Quinn 1990; Zelenitsky and Hills 1997; Bray 1999; Zelenitsky and Therrien 2008; Jackson and Varricchio 2010, 2016, 2017; Zelenitsky et al. 2017a, b; Voris et al. 2018).

However, two Upper Cretaceous North American strata, the Hell Creek Formation and the Lance Formation, have yielded few egg remains (Carpenter 1982; Jackson and

Varricchio 2016). Both the Hell Creek and the Lance formations have produced numerous skeletal remains (e.g., Lehman et al. 2006; Brown et al. 2022; Ponstein et al. 2024), however, temporally equivalent formations, such as the Willow Creek and St. Mary River formations in Canada, have yielded both skeletal and oological remains (Brown et al. 2015; Zelenitsky et al. 2017a; Voris et al. 2018). The lack of egg remains in the Hell Creek and Lance formations has been attributed to soil drainage and soil pH (Carpenter 1982). Relatively recently, the first oological remains from the Hell Creek Formation have been described (Jackson and Varricchio 2016), but eggshell remains from the Lance Formation remain undescribed. Here, we provide the first description of an eggshell fragment from the Lance Formation of Wyoming.

Institutional abbreviation.—MAB, Oertijdmuseum, Boxtel, the Netherlands.

Other abbreviations.—CL, continuous layer; ML, mamillary layer.

Material and methods

The eggshell (MAB16636) was recovered by RHBf (4th author) in 2022 during sieving of a prolific microsite in the Lance Formation located near Lusk in eastern Wyoming, USA (Fig. 1). The exact location remains undisclosed due to the vulnerability of the site. Detailed locality information can be requested from the authors. This microsite has yielded remains of mammals, fish, turtles, crocodiles, and dinosaurs. A single radial section of MAB16636 was made, which was subsequently scanned using a Zeiss Axio Scan. Z1 v1.0, using 10× and 20× objective lenses. An Axio Scan can be used for automatic imaging to create a virtual slide of histological sections of fossil eggshell. Zeiss Zen Lite (Blue edition) version 3.2 software was used to subsequently photograph and measure the eggshell. Scanning electron micrographs were made with a JEOL Neoscope JCM-6000 tabletop SEM and a ZEISS EVO 15 SEM.

Systematic palaeontology

Oofamily Ovaloolithidae Mikhailov, 1991

Oogenus *Ovaloolithus* Zhao, 1979

Type species: *Ovaloolithus chinkangkouensis* Zhao & Jiang, 1974 amended Zhao, 1979. Laiyang Basin, China; Jingangkou Formation, Coniacian–Campanian.

Ovaloolithus oosp.

Figs. 2, 3.

Material.—The eggshell (MAB16636) from the Upper Cretaceous, Lance Formation, USA, eastern Wyoming, near Lusk.

Description.—The eggshell fragment is small (<1 cm²), with a smooth outer surface (Fig. 2A). The minimum thickness of the eggshell is 1.1 mm, as the fragment has suffered minor abrasion, particularly on the inner surface. The eggshell consists of two layers: a mammillary and a continuous (Fig. 2B₁). The ML extends to about half the thickness of the eggshell, with a ratio of 1:1 between the ML and CL (Fig. 2B₁). A relatively distinct contact between the ML and CL is accentuated by a brown horizontal line (Fig. 2B₁). The ML consists of closely packed shell units (Fig. 3A₁, A₄) that are wedge-like with a radial-tabular ultrastructure. Only the ML shows vertical boundaries between adjacent shell units—these are lost in the CL such that the shell units become indistinguishable from each other. The CL shows considerable brown horizontal lineation. The SEM microphotographs (Fig. 3A₅) show cleavage of the eggshell in some parts where the brown lineation is visible under normal and polarized light. Faint horizontal accretion lines are visible in both the ML and CL (Fig. 2). Part of a pore can be seen in radial section (Fig. 2B₁). The pore is circular, and appears oriented obliquely. However, SEM microphotographs (Fig. 3A₃) confirm that the pores in MAB16636 are vertically oriented, with slightly undular canal walls, possibly affected by infill.

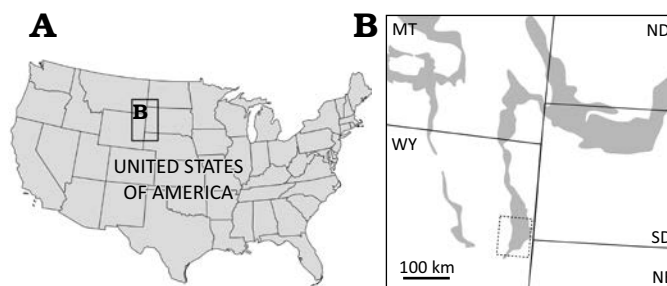


Fig. 1. Map of United States of America (A) with locality of the eggshell in eastern Wyoming (B). Lance Formation outcrops indicated in grey.

Remarks.—The abovementioned characteristics correspond to the description of the angustispherulitic morphotype, and in combination with the smooth outer surface and vertical pores, MAB16636 can be placed within Ovaloolithidae (Mikhailov 1991, 1997). Two oogenes are known in this oofamily: *Ovaloolithus* Zhao, 1979, and *Minioolithus* Wu et al., 2024. The former oogenes contains twelve oospecies, we herein disregard ?*Ovaloolithus weiqiaoensis* Yu, 1998, and ?*Ovaloolithus huangtulingensis* Yu, 1998, due to their insufficient description and uncertain affinities (Zhao et al. 2015), distributed in the Upper Cretaceous outcrops of China, Mongolia, and USA. *Minioolithus* is a recently erected oogenes from the Tangbian Formation (Santonian–Campanian) of China (Wu et al. 2024). MAB16636 can easily be distinguished from *Minioolithus*, as this ootaxon shows distinct ornamentation and is very thin for an ovaloolithid oospecies (0.13–0.35 mm). The characteristics of MAB16636, therefore, better fit *Ovaloolithus* sensu Mikhailov (1997).

Two oospecies of *Ovaloolithus* are known from USA: *Ovaloolithus utahensis* Bray, 1999, and *Ovaloolithus tenuis* Bray, 1999. Both are from the Maastrichtian North Horn Formation of Utah. MAB16636 can be distinguished from both *Ovaloolithus utahensis* (1.42–1.68 mm) and *Ovaloolithus tenuis* (0.43–0.58 mm) based on eggshell thickness. Similarly, MAB16636 can be distinguished from the following Asian oospecies due to eggshell thickness: *Ovaloolithus chinkangkouensis* (Zhao & Jiang, 1974) (2.60 mm in Zhao et al. 2015), *Ovaloolithus tristriatus* (Zhao & Jiang, 1974) (2.40 mm in Zhao et al. 2015), *Ovaloolithus mixtistriatus* (Zhao & Jiang, 1974) (2.50 mm in Zhao et al. 2015), *Ovaloolithus monostriatus* (Zhao & Jiang, 1974) (1.50 mm in Zhao et al. 2015), *Ovaloolithus (Pinnatoolithus) shitanensis* (Fang et al., 2009) (1.80–2.60 mm in Zhao et al. 2015), *Ovaloolithus (Pinnatoolithus) nanxiogensis* (Fang et al., 2009) (1.70 mm in Zhao et al. 2015), *Ovaloolithus (Pinnatoolithus) sangequanensis* (Fang et al., 2009) (3.00 mm in Zhao et al. 2015), and *Ovaloolithus turpanensis* Zhang & Wang, 2010 (1.88 mm in Zhang and Wang 2010). Only two ovaloolithid oospecies show overlap with MAB16636 in eggshell thickness: *Ovaloolithus laminadermus* (Zhao & Jiang, 1974) (0.60–1.20 mm in Zhao and Jiang 1974; 0.90 mm in Zhao et al. 2015) and *Ovaloolithus dinornithoides* Mikhailov, 1994 (1.10–1.80 mm in Mikhailov

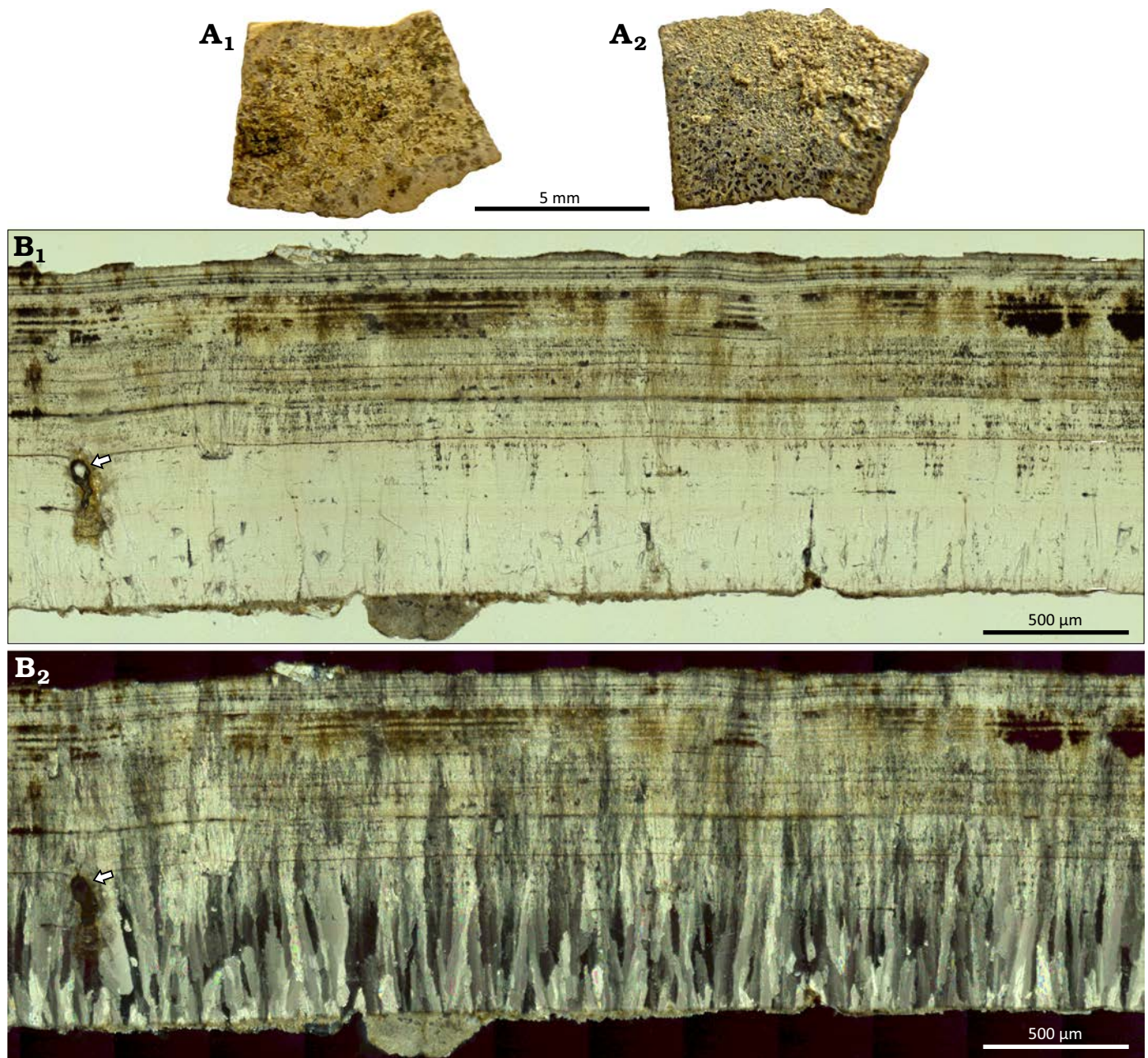


Fig. 2. Eggshell MAB16636 from the Maastrichtian Lance Formation, near Lusk, eastern Wyoming, USA. **A.** Outer (A_1) and inner (A_2) surface morphology. **B.** Radial section of eggshell, in normal (B_1) and polarized (B_2) light. Note the pore (white arrow) near the transition between the mammillary layer (ML) and continuous layer (CL).

1994). However, direct comparisons of MAB16636 with other ovaloolithid oospecies solely based on eggshell thickness are problematic and exemplified by Mikhailov (1994), who points out that for *Ovaloolithus dinornithoides*, the full eggshell range is 1.1–1.8 mm, but that the standard ranges are 1.5–1.8 mm and 1.3–1.6 mm, respectively. For *Ovaloolithus chinkangkouensis*, Mikhailov (1994) adds similar variation in eggshell thickness ranges, as the standard range for this oospecies is 2.2–3.0 mm, whereas the full range within a single egg is 1.4–3.0 mm. Therefore, for most ovaloolithid oospecies, the full ranges of eggshell thickness remain unexplored and difficult to compare to

MAB16636. In addition, MAB16636 only represents a small fraction of the full egg. A thickness range cannot be established for this specimen.

MAB16636 can be further distinguished from all Asian ovaloolithid oospecies based on the lack of ornamentation (Young 1954; Zhao and Jiang 1974; Mikhailov 1994; Fang et al. 2009; Zhang and Wang 2010; Zhao et al. 2015), but Wu et al. (2024: table 1) report for most ovaloolithid oospecies that the ornamentation is unknown. However, Young (1954), Zhao and Jiang (1974), Mikhailov (1994), and the radial sections in Zhao et al. (2015) clarify the presence of weak to strong nodose/sagenotuberculate ornamentation in the

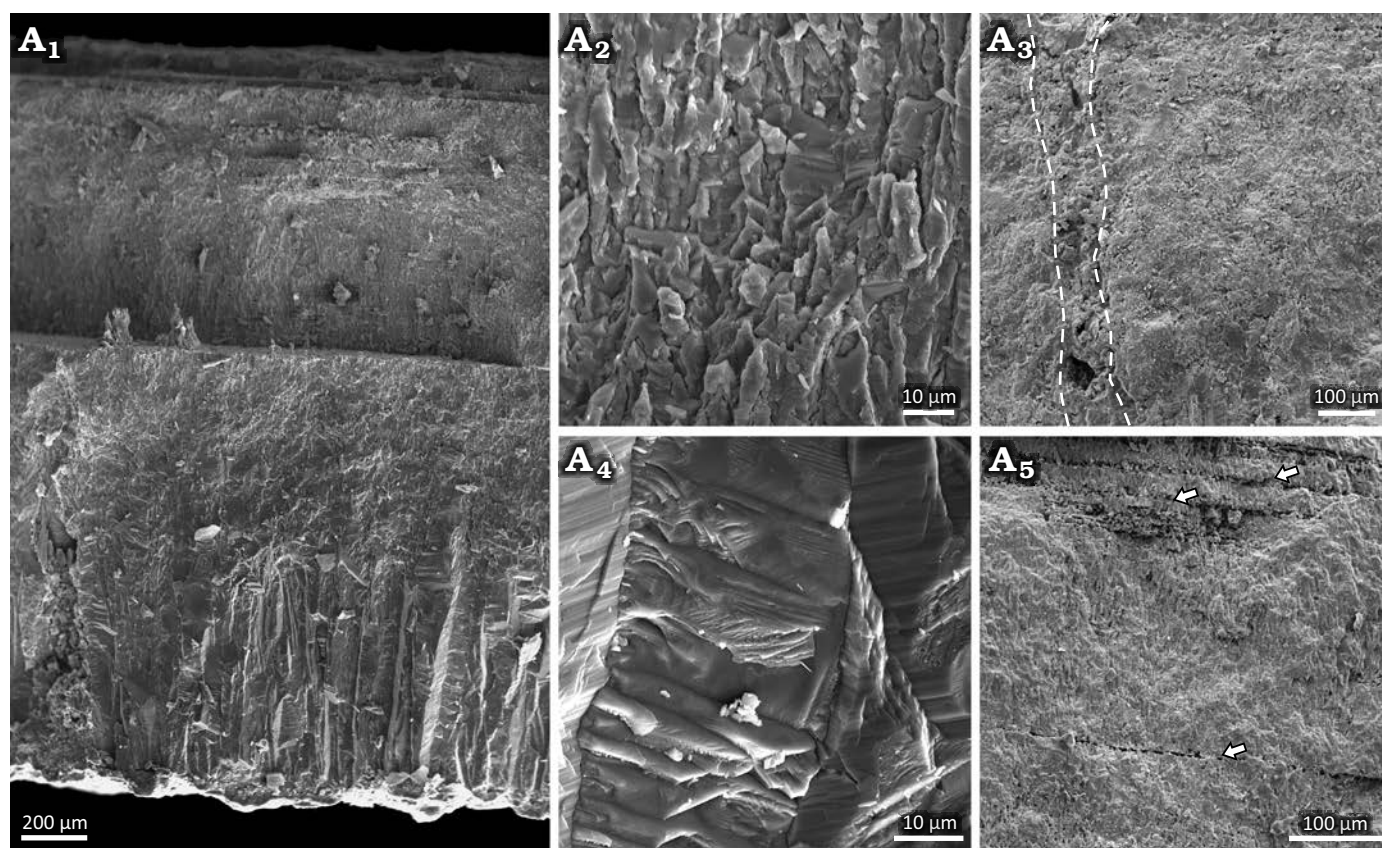


Fig. 3. SEM microphotographs of eggshell (MAB16636) from the Maastrichtian Lance Formation, near Lusk, eastern Wyoming, USA, including an overview of the eggshell (A₁); A₂, close-up of the continuous layer (CL); A₃, the CL and a pore highlighted by a dashed line; A₄, the wedged structure of the mammillary layer (ML); A₅, the cleaved layers near the outer surface, highlighted by arrows. Note that in A₁, one of the cleavage planes caused an uneven break, such that part of the middle of the eggshell became exposed.

majority of ovaloolithid oospecies. An exception appears to be *Ovaloolithus* (*Pinnatoolithus*) *nanxiongensis*, which Fang et al. (2009) report to be relatively smooth and not very undulating in thin section. However, we would argue that the description does not match the figured thin section by Fang et al. (2009), which shows a significantly more undulating outer surface than MAB16636, *Ovaloolithus uta-hensis*, or *Ovaloolithus tenuis* (Bray 1999). Additionally, *Ovaloolithus dinornithoides* consists of a complete egg that shows variation across the eggshell surface, with the majority of eggshell not expressing any ornamentation (Mikhailov 1994). Significant variation in the presence or absence of ornamentation is therefore to be expected within Ovaloolithidae.

Most ovaloolithid oospecies, including MAB16636, show a ratio of 1:1 between the ML and CL. Exceptions include *Ovaloolithus* (*Pinnatoolithus*) *shitangensis* (2:5, Fang et al. 2009), *Ovaloolithus* (*Pinnatoolithus*) *nanxiongensis* (1:3, Fang et al. 2009), *Ovaloolithus* (*Pinnatoolithus*) *sangequanensis* (1:3, Fang et al. 2009), and *Ovaloolithus turpanensis* (1:3, Zhang and Wang 2010). The variation in this ratio throughout the entire eggshell, however, remains unexplored for this oofamily.

Although weakly ornamented, *Ovaloolithus laminadermus* and *Ovaloolithus dinornithoides* are most comparable

to MAB16636. Comparisons are hindered by the limited description of the ultrastructure of most ovaloolithid oospecies, as they are mainly differentiated by the horizontal lineation present throughout the eggshell. Wang et al. (2022) determined that this lineation is unsuitable for distinguishing ovaloolithid oospecies. These lines are numerous in MAB16636, and at least some are the result of weathering based on the SEM images (Fig. 3A₅), although the majority of the lineation may in fact be thermally matured organic matter (Choi et al. 2021, 2025). If these lines are dependent on preservation and variable within a single egg or clutch (Wang et al. 2022), then the remaining characteristics of most ovaloolithid oospecies overlap (see Wu et al. 2024: table 1). Therefore, we propose that this oofamily is in need of revision, in accordance with Wang et al. (2022).

We argue that MAB16636 cannot be assigned to a specific oospecies within Ovaloolithidae, as (i) thickness ranges within the oofamily have not been thoroughly explored, (ii) ornamentation can vary significantly within a single egg, and (iii) diagnostic lineation may depend on preservation and vary considerably, leading to considerable variation within this oofamily that complicates oospecies assignment. MAB16636 consists of only a single eggshell fragment, which we assign to *Ovaloolithus* oosp., and not to a specific oospecies within Ovaloolithidae.

Discussion

Late-stage embryonic remains are the primary and most trustworthy source for inferring links between parataxonomy and taxonomy. Few dinosaurian taxa have been confidently attributed to ootaxa (Choi et al. 2022). There are no ovaloolithid eggs known preserving embryonic remains, such that an unambiguous link with a dinosaur taxon cannot be made. Mikhailov (1997) describes ovaloolithid eggs as most reminiscent of spheroolithid eggs, that are ascribed to ornithopod dinosaurs (Moreno-Azanza et al. 2014; Van der Linden et al. 2024), with the former similarly interpreted as ornithopod eggs. This is further supported by several stratigraphic layers in Mongolia which yield only ovaloolithid eggs and lambeosaurine ornithopods (Mikhailov 1997). However, lambeosaurine hadrosaurs are effectively unknown from the Lance Formation (see Wegwesier et al. 2003 and Rolleri et al. 2020 for possible exceptions) or the contemporaneous Hell Creek Formation. Therefore, ovaloolithid eggs could be, similar to spheroolithid eggs, taxonomically more inclusive, and thus may encompass all of Ornithopoda, or even Ornithischia. The latter suggestion may be supported by Sochava (1972), who describes ovaloolithid eggshell in association with embryonic metatarsals of a ceratopsian dinosaur similar to *Leptoceratops* or *Protoceratops*. However, recent description of a *Protoceratops* clutch revealed that ceratopsian eggs consist of non-biomineralized, soft eggshell (Norell et al. 2020).

Recently, Wu et al. (2024) argued for a different taxonomic link, and instead proposed a non-avian theropod affinity for Ovaloolithidae based on the eggshell characteristics and a novel phylogenetic analysis of dinosaur eggs. Non-avian theropod remains are common in the Lance Formation (Brown et al. 2022). Caenagnathids (Pu et al. 2017), alvarezsaurids (Agnolin et al. 2012), dromaeosaurids (Grellet-Tinner and Makovicky 2006), and troodontids (Varricchio et al. 2002) are known to have produced significantly different eggs from Ovaloolithidae. No eggs unambiguously attributed to ornithomimosaurs or tyrannosaurs are known, such that ovaloolithid eggs may be parataxonically linked to either group. Due to the lack of embryonic remains associated with ovaloolithid eggs, MAB16636 is herein tentatively referred to either ornithopods or non-avian theropods until unambiguous evidence is presented.

The ambiguous link between ovaloolithid eggs and a particular non-avian dinosaur prevents clear biogeographic implications. A similar claim as made by Simon et al. (2019) regarding the presence of a giant oviraptorosaur in both North America and Asia based on the presence of *Macroelongatoolithus* cannot be made. However, some tentative but interesting observations can be made. The North American record of Ovaloolithidae, albeit sparse, is restricted to the Maastrichtian (Bray 1999; this study). However, in Asia, ovaloolithid eggs are known from possibly the Coniacian till the Maastrichtian (Wu et al. 2024), with a particularly rich record in the Campanian–Maastrichtian

(Wan et al. 2007; Wang et al. 2022; Zhang et al. 2023; Wu et al. 2024). It, therefore, can be hypothesized that the parental taxon of ovaloolithid eggs migrated from Asia into Laramidia prior to the Maastrichtian.

Morrison et al. (2025) recently recovered that *Tyrannosaurus* possibly originated from a pre-Maastrichtian Asian ancestor, such that a similar dispersal route is postulated for the origins of Tyrannosaurini as hypothesized here for Ovaloolithidae. This could be interpreted as additional, albeit highly speculative, evidence that ovaloolithid eggs may be linked with tyrannosaurine theropods, given the similar dispersal route and timing. The Lance and Hell Creek formations include *Ornithomimus* and/or *Struthiomimus*, with the exact identifications of the specimens still unresolved (Stein 2019). Testing the link of ovaloolithid eggs to these ornithomimosaurs from a biogeographic perspective is hampered by the poor resolution of ornithomimid phylogenies (e.g., Tsogtbaatar et al. 2017; Serrano-Brañas et al. 2025). Therefore, no clear dispersal origin can be reconstructed, such that no tentative additional evidence can be provided for a simultaneous dispersal event of ovaloolithid eggs, through the parental taxon, and ornithomimosaurs, linking them to each other. A saurolophine hadrosaurid link is, similar to the tyrannosaur hypothesis, a possibility for ovaloolithid eggs based on the origins of *Edmontosaurus annectens*. Edmontosaurini most likely originated in Asia as well, such that a similar dispersal route can be postulated (Xing et al. 2017; Alarcón-Muñoz et al. 2023). However, as aforementioned, a theropod origin is better supported for ovaloolithid eggs (Wu et al. 2024). Therefore, the link between ovaloolithid eggs and saurolophine hadrosaurs is not well supported. This is evidenced by the differing eggshell characteristics of saurolophine eggs, as exemplified by *Maiasaura* (Hirsch and Quinn 1990; Zhu et al. 2022) and potentially *Saurolophus* (Dewaele et al. 2015).

Although Carpenter (1982) reported the presence of eggshell from the Lance Formation, none of the material was parataxonically identified. Jackson and Varricchio (2016) identified eggshell material from the Hell Creek Formation, including theropod, ornithopod (spheroolithid), turtle, and crocodile egg material. As more eggshell material is known from the Lance Formation than reported in the present study, see Carpenter (1982), future studies should focus on the oological diversity present in this formation.

Conclusions

The first eggshell from the Maastrichtian Lance Formation is described here, and is most comparable to the oofamily Ovaloolithidae, and is assigned here to *Ovaloolithus* oosp. Although no unambiguous link between ovaloolithid eggs and a dinosaurian parent exist, we tentatively assign the eggshell fragment to either ornithopod or non-avian theropod dinosaurs. As eggshell material is very scarce from

both the Hell Creek and Lance formations, this new eggshell from Wyoming adds significantly to the description of Maastrichtian oological material from North America.

Acknowledgements

The authors thank the ranchers for their hospitality to conduct fieldwork on their land. We thank Jean-Pierre Cavigelli (Tate Museum, Casper, USA) for aiding the fieldwork. We thank Leonard Bik and Richard Wessels (Utrecht University, the Netherlands) for producing and scanning the microslides. We thank Wilma Wessels, Ivo van der Beek and Eric W.G. Hellebrand (all Utrecht University, the Netherlands) for aiding with scanning electron microscopy at. Finally, we thank Darla K. Zelenitsky (University of Calgary, Calgary, Canada), Cassius Morrison (University College London, London, UK) and the anonymous reviewers for their detailed, helpful and constructive feedback on earlier versions of this manuscript.

Editor: Daniel Barta

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